

Aerial Arthropod Communities of Native and Invaded Forests, Robinson Crusoe Island, Chile

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ABSTRACT Invasive species significantly contribute to biological change and threaten biodiversity, with a growing body of evidence that plant invasions affect higher trophic levels. We explored the relative importance of plant invasion and forest structure on aerial arthropod abundance, diversity, and composition on Robinson Crusoe Island, Chile. We used flight intercept traps to sample aerial arthropods within distinct canopy strata of native and invaded forests over 3-mo periods in 2006 and 2007. Arthropod abundance and diversity were higher in native than invaded forest, and arthropod communities were distinct between forest types. In both forest types, arthropod abundance was highest in the lower canopy, and canopy strata exhibited some differences in arthropod community composition. Several morphospecies were distinctly associated with each forest type. The strong differences in aerial arthropod communities associated with the invasion of native forest by non-native plants may affect other trophic levels, such as insectivorous birds. Steps to stop invasive plant spread and to restore native forest composition and structure are needed to safeguard the integrity of native communities, from plants to higher-level consumers.

KEY WORDS arthropod communities, Juan Fernández Archipelago, plant invasion, trophic levels

Human activities have accelerated the rate of species introductions, with serious consequences (Mack et al. 2000). Species introductions can have disproportionately strong impacts on oceanic islands, where native populations are generally smaller, more isolated, and have evolved with different evolutionary pressures than continental biota (Reaser et al. 2007). Robinson Crusoe Island is a case in point. This volcanic island is part of the Juan Fernández Archipelago, Chile (33°40' S, 78°47' W) and is internationally recognized for its high endemism rate and for the severe threats posed to these species by introduced mammals, plants, and insects (Perry 1984, Allen 1985). More than 90% of Robinson Crusoe has been degraded through human-mediated changes (Meza 1989), and loss of intact native forest and endemic plant species continues (Danton 2004). For example, maqui (*Aristotelia chilensis*) trees and elm-leaf blackberry (*Rubus ulmifolius*) shrubs, introduced in 1864 and 1927, respectively, invade quickly (Greimler et al. 2002) and may replace one half of the remaining native montane forest within 75 yr if forest restoration efforts are not successful (Dirnböck et al. 2003).

The effects of plant invasion on forest arthropod communities are receiving increasing attention, and studies indicate that shifts from native to invasive dominant plant species can reduce abundance and

diversity of canopy arthropods and even change species composition (Greenwood et al. 2004, Durst et al. 2008, Gerber et al. 2008, Heleno et al. 2008, however, see Proches et al. 2008). Plant invasions may affect light stratification, temperature, humidity, wind, and forest composition that can alter arthropod distribution and established trophic webs (Barbosa and Wagner 1989, Schowalter 2000). Investigation of the vertical stratification of arthropods in the forest canopy is a relatively new field and is growing through methodological advances (Basset et al. 2003). In tropical forests, arthropod communities exhibit strong vertical stratification because of distinctive upper canopies and associated niches (Basset et al. 2003). The influence of forest strata on arthropod communities of temperate forest canopies is less clear yet is increasingly recognized as important to forest management and conservation (Ulyshen and Hanua 2007, Vance et al. 2007).

Arthropods provide an ideal model system to examine the effects of plant invasions on higher trophic levels. Their life history traits such as small body size, high reproductive rates, and short generation time translate into quick, easily measurable responses to environmental change compared with other organisms (Schowalter 2000). In addition, they are an important intermediate trophic level within food webs: they choose what and where to eat, and are a component of the diet of many animals. Therefore, understanding arthropod responses to plant invasion

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helps expand our understanding of impacts on higher trophic levels.

We examined the relative importance of plant invasion and forest structure on aerial arthropod communities of Robinson Crusoe Island. Our first objective was to assess potential differences between invaded and native forests. We hypothesized that, because of their simplified composition, invaded forests would have lower insect diversity and abundance and a distinct community composition compared with intact native forest. Our second objective was to examine the influence of canopy strata on arthropod abundance and composition. We expected the upper canopy to have lower arthropod abundance and distinct arthropod communities compared with the lower canopy, because it is more exposed to the wind and elements and thus may be a less favorable habitat. By examining strata in invaded and native forests, we were able to assess the interaction between these factors.

Materials and Methods

We sampled arthropods in two distinct forest types, native and invaded forest, at 210–250 m elevation on Robinson Crusoe Island. Native lower montane forest is dominated by endemic luma (*Myrceugenia fernandeziana*) trees up to 15 m tall; total tree cover is 70–100%. In these forests, tree ferns are scattered, shrubs are rare, and ground and climbing ferns are abundant. Invaded forest has fewer large trees, although maqui forms a low tree layer at ≈ 6 m height. Total cover is 90–100%, with limited herbs and mosses and scattered elm-leaf blackberry shrubs (Greimler et al. 2002).

We used three-dimensional flight interception traps (modified from Wilkening et al. 1981) to sample the aerial arthropod community from September through mid-November 2006 and 2007. We limited sampling to a single drainage to minimize differences in abiotic factors. This drainage represents $\approx 30\%$ of the island's forests and harbors declining populations of endemic species (Meza 1989; Honeyman et al. 2005). We hung traps at four locations (vertical arrays) per forest type to sample three canopy strata: 1.35–2.50 (lower canopy of both forest types), 3.50–6.00 (mid-canopy of native forest; upper canopy of invaded forest), and 7.50–9.30 m (upper canopy of native forest). In total, therefore, we installed 20 traps. We placed traps randomly within pre-established 1-ha plots where regular flowering phenology and animal population census monitoring occurs (Chilean Forestry Service, Universidad de Chile). We collected arthropods under permits from the National Forestry and Agriculture Departments of Chile (Corporación Forestal Nacional and Servicio de Agrícola y Ganadero) and placed voucher specimens at the Natural History Museum of Chile (Museo Nacional de Historia Natural).

We collected samples biweekly or immediately after heavy rains, whichever came first. After collecting

the arthropod samples, we performed routine maintenance or replacement as needed and reinstalled traps in their original positions. We sorted, measured, and identified arthropods to family and morphospecies. We calculated the mean abundance of each morphospecies in each trap, averaging across sample periods within a given year, because our primary interest was in making comparisons between forest types and among vertical levels (rather than analyzing changes through time within a year).

Comparisons Between Forest Types and Strata. We calculated alpha, beta, and gamma diversity for each forest type and height class. Alpha diversity is the average number of morphospecies per trap, beta diversity is the total number of morphospecies observed divided by the average richness per trap (i.e., gamma diversity divided by alpha diversity), and gamma diversity is the total number of morphospecies observed.

Alpha diversity was compared between forest types with *t*-tests. Beta and gamma diversities were compared qualitatively but not tested statistically because of low sample sizes. We compared arthropod richness between forest types with species rarefaction curves and their associated 95% confidence intervals (specaccum function, vegan package, R 2.8.1). We estimated species richness by using the Chao estimator to extrapolate from the observed samples (specpool function, vegan package, R 2.8.1).

We used fixed factor general linear models to examine the effects of forest type and canopy strata on total arthropod abundance (sum of the mean numbers of individuals per morphospecies per sampling period) and community composition. We analyzed each year separately. Analyses were conducted sequentially: we began by testing if there were significant differences among our five groups (combinations of forest type and canopy height). If this effect was statistically significant, we proceeded to test a series of a priori contrasts: (1) forest type, (2) canopy strata within the invaded forest, and (3) canopy strata within the native forest. We included trap location as a blocking factor in all analyses to account for potential spatial autocorrelation among samples obtained from a given vertical sampling array. Analyses were conducted using PERMANOVA, a distribution-free analytical method analogous to multivariate analysis of variance (MANOVA) (Anderson 2001, McArdle and Anderson 2001, adonis function, vegan package, R 2.8.1). We used the Bray-Curtis dissimilarity measure and 9,999 permutations during all analyses. For analyses of community composition, we focused on common species (those identified from $\geq 15\%$ of traps) and standardized data by species maxima and trap totals before calculating the Bray-Curtis dissimilarity matrix. Treatment effects on composition were visualized with nonmetric multidimensional scaling ordinations (NMDS; metaMDS function, vegan package, R 2.8.1). We performed NMDS using 100 random starting configurations for each of one to five dimensions and examined scree plots to select the appropriate dimensionality for data.

Table 1. Summary diversity statistics for aerial arthropod morphospecies

	N	Diversity measure		
		Alpha	Beta	Gamma
2006				
Native forest	12	18.9 (6.4)	4.6	87
Invaded forest	8	12.0 (3.8)	3.6	43
All	20	16.2 (6.4)	6.3	102
2007				
Native forest	12	21.7 (5.6)	3.5	75
Invaded forest	8	17.3 (3.9)	3.1	53
All	20	19.9 (5.3)	4.1	87
Grand total	40	18.0 (6.1)	7.5	135

The no. of traps sampled in native and invaded forest in 2006 and 2007 is reported as *N*. Alpha diversity is the average (SD) no. of morphospecies per trap, beta diversity is the total no. of morphospecies observed divided by the average richness per trap, and gamma diversity is the total no. of morphospecies observed.

Significant a priori contrasts from the compositional analysis were followed by indicator species analysis (ISA; Dufrene and Legendre 1997) to identify morphospecies closely and uniquely associated with treatments. The relative abundance and relative frequency of each morphospecies were used to calculate its indicator value (IV), and *P* values were generated from 9,999 Monte Carlo permutations. We conducted separate ISAs for each year and used meta-analytical techniques to combine results (R 2.8.1; Bakker 2008). We considered morphospecies with $P < 0.05$ and $IV > 25$ for biological significance.

Results

We collected a total of 6,902 arthropods and identified 135 morphospecies representing 69 families. Just over 73% of the arthropods belonged to the subfamily Scolytinae (Coleoptera: Curculionidae) and 6% to the midges (Diptera: Chironomidae). On average, we collected 137 individuals per trap (SE = 33.0) in 2006 and 208 individuals per trap (SE = 196.9) in 2007. Alpha diversity was higher in native than invaded forest in both years (2006 $t = 3.05$, $df = 18$, $P = 0.007$; 2007 $t = 2.09$, $df = 18$, $P = 0.051$). Gamma diversity was also higher in native than

invaded forest; overall diversity (135 morphospecies) was 32–55% higher than diversity in either year (Table 1). Beta diversity was highest when all samples were considered together, reflecting the greater diversity of locations sampled.

Species rarefaction curves showed that alpha diversity differed among forest types at larger sampling intensities (≥ 4 traps in 2006, ≥ 7 traps in 2007) but not at smaller intensities (Fig. 1). Species were still accumulating after eight traps; we estimated the total aerial arthropod richness (SE) to be greater in native than invaded forest in both years (2006: native 169, 33.6; invaded 88, 25.5; 2007: native 99, 12.7, invaded 76, 20.6).

Total aerial arthropod abundance differed among treatments and was much greater in native than invaded forest (Fig. 2; Table 2). Abundance decreased with increasing height of canopy strata within native forest in both years and within invaded forest in 2007.

Community composition differed among treatments, with a priori contrasts indicating distinct communities in native and invaded forest (Fig. 3; Table 2). Composition in lower canopy strata was distinct in both forest types in 2007.

Meta-analysis of 2006 and 2007 ISA results identified six morphospecies as strong indicators of native forest and two as strong indicators of invaded forest (Table 3). Similar to dominant orders within samples, these indicator morphospecies represented the orders Coleoptera and Diptera.

Discussion

Invaded forests on Robinson Crusoe Island contain lower aerial arthropod diversity and abundance and have distinct arthropod communities compared with native forests. One third of native forest on the island has already been lost, and the remaining forest continues to be converted to simplified stands of invasive maqui and elm-leaf blackberry (Dirnböck et al. 2003). Our findings suggest that unchecked plant invasions on the island have serious implications for the endangerment and extinction of endemic island species, many of which have their global populations confined to the last remaining forested reaches of Robinson

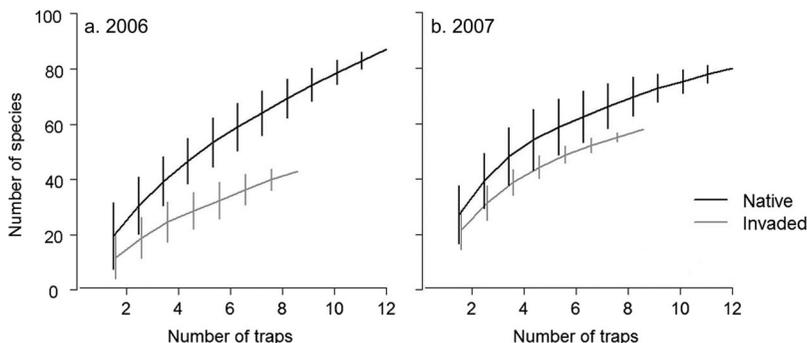


Fig. 1. Species rarefaction curves based on aerial arthropod sampling in native and invaded forests. Curves fit 2006 data (a) and 2007 data (b). Bars represent 95% confidence intervals.

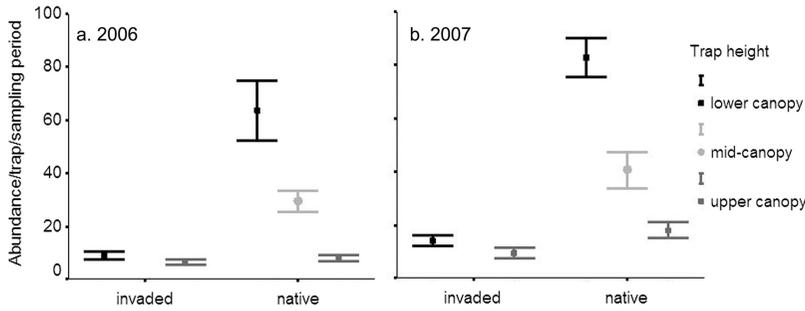


Fig. 2. Mean (SE) abundance of aerial arthropods in native and invaded forest in 2006 (a) and 2007 (b). a priori contrasts among forest types and canopy strata to examine abundance are summarized in Table 2. Equal number of traps were placed in each unique forest type-canopy strata combination ($n = 4$).

Crusoe. Other studies from around the globe report similar consequences of plant invasions (Majer and Recher 1999, Greenwood et al. 2004, Southwood et al. 2005, Durst et al. 2008).

We detected some interannual differences in aerial arthropod diversity and in their abundance and composition within forest strata. Limited data available at sea level suggest $\approx 20\%$ lower rainfall during sampled months in 2007 than 2006. Heavier 2006 rains may have impacted certain arthropod species' growth and survival and therefore community composition. A taller, more diverse native canopy may more effectively buffer the lower canopy from rains than does the invasive canopy, providing a possible explanation for similar patterns of aerial arthropod abundance and diversity in native but not invaded forest strata between years. However, a more comprehensive assessment of interannual variability would require a longer dataset.

Using meta-analysis of ISA results allowed us to identify morphospecies that were representative of native and invaded forests despite climatic fluctuations between years. Largely, indicators were identified to morphospecies only; species identities are currently unavailable. However, one morphospecies consistently associated with invaded forest was identified as Fuller's rose beetle (*Asynonychus cervinus*, Coleoptera: Curculionidae), a cosmopolitan non-native species that consumes foliage. A morphospecies of bark beetle (Coleoptera: Curculion-

idae subfamily Scolytinae) was a very strong indicator of native forest and also dominated the arthropods in terms of number of individuals sampled. Further study is needed to identify the species involved and to investigate how consistently bark beetles dominate native habitat or whether our sampling coincided with seasonal peaks in bark beetle flight activity.

Through their impacts on arthropod communities, plant invasions may cause a cascade of bottom-up effects on other trophic levels. For example, insectivorous birds with specialized foraging techniques (Unno 2002) or preferences for specific tree species or structure (Rodewald and Abrams 2002, Walker 2008) may be disproportionately impacted in forests undergoing dominant species replacements. On Robinson Crusoe Island, the endemic Juan Fernández Firecrown (*Sephanoides fernandensis*) is closely tied to native forests (Meza 1989, Roy et al. 1999). This hummingbird is critically endangered (BirdLife International 2008) and habitat changes and food limitation have been implicated in its decline (Colwell 1989, Meza 1989). Hummingbirds have high metabolic demands and, in addition to nectar, feed on arthropods for additional sources of amino acids and energy (Gass and Montgomery 1981, Martínez del Río 1994, Stiles 1995). Examinations of firecrown diet through stomach sampling and foraging behavior confirm that they consume the arthropods found in our study. Their potential

Table 2. Results from PERMANOVA analyses examining the effects of treatment (combinations of forest type and canopy strata) and location within forest type on abundance and composition of aerial arthropods in 2006 and 2007

Treatment	Abundance				Composition			
	2006		2007		2006		2007	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Treatment	26.11	<0.001	38.58	<0.001	2.07	<0.001	2.56	<0.001
Forest type	41.89	<0.001	80.34	<0.001	4.99	<0.001	4.6	<0.001
L versus U in invaded forest	2.19	0.150	7.92	0.006	0.54	0.922	1.82	0.021
L versus U in native forest	51.28	<0.001	60.20	<0.001	1.64	0.072	2.38	0.003
L versus M in native forest	10.64	0.004	18.88	<0.001	1.28	0.206	1.99	0.012
M versus U in native forest	28.63	<0.001	20.04	<0.001	1.19	0.264	1.35	0.147
Location	1.51	0.240	1.42	0.268	1.06	0.373	1.55	0.006

a priori contrasts are inset beneath the treatment effect, and canopy strata are abbreviated as L (lower), M (mid), and U (upper). $P \leq 0.05$ are shown in italics.

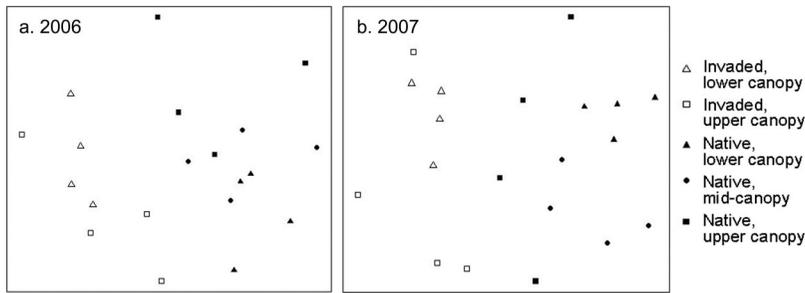


Fig. 3. NMDS ordinations based on 32 morphospecies in 2006 (a), and 51 morphospecies in 2007 (b). Shading represents forest type, and shape represents trap height within canopy. Both solutions had two dimensions ($stress_{2006} = 18.48$; $stress_{2007} = 23.10$). a priori contrasts among forest types and canopy strata to examine composition are summarized in Table 2.

prey followed the same trends described above for the full complement of data, with lower diversity and abundance in invaded forest compared with native forest (E.H., unpublished data; Insitutional Animal Care and Use Committee Protocol #4142-01; permit for collection from National Forestry and Agriculture Departments of Chile). Although this study was not designed to assess the responses of consumers to aerial arthropods, our initial observations suggest that plant invasion may negatively impact multiple trophic levels of Robinson Crusoe’s unique forest ecosystem.

In summary, we found an association between plant invasion and reduced aerial arthropod abundance and diversity and found distinct arthropod community composition between forest types. Although we were unable to comprehensively sample canopy insects, the observed trends suggest that plant invasions have affected higher trophic levels within the forest. In <150 yr, maqui and elm-leaf blackberry have dramatically altered the landscape and natural communities of Robinson Crusoe Island. A management program that restores native, multistrata forests is needed to curb further losses of the unique and ecologically important native system of the island. Because terrestrial arthropods are diverse and important in the diet of many taxa (Tallamy 2004), we also conclude that management

plans that safeguard arthropod communities would protect biodiversity of multiple trophic levels.

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Table 3. Results from meta-analysis of indicator species analysis

	Order: Family	Mean IV	P combined
Native forest	Coleoptera: Curculionidae subfamily Scolytinae	93	<0.001
	Coleoptera: Staphylinidae	79	<0.001
	Diptera: Anisopodidae	75	<0.001
	Coleoptera: Aderidae	52	<0.001
	Diptera: Simuliidae	47	<0.001
	Coleoptera: Cavognathidae	46	<0.001
Invaded forest	Coleoptera: Curculionidae	50	<0.001
	Coleoptera: Bostrichidae	59	0.003

Morphospecies with high relative abundances and frequencies in both 2006 and 2007 were examined. Listed morphospecies are strong indicators of native and invaded forests, as shown by high mean indicator values (IV) and low P values. Morphospecies are described by Order and Family.

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